

Enigmatic distribution: first record of a hitherto New World planthopper taxon from Japan (Hemiptera, Fulgoroidea, Delphacidae, Plesiodelphacinae)

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Abstract

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Burnilia japonica sp. n. of the delphacid subfamily Plesiodelphacinae from southern Japan (Kyushu, Yakushima, Okinawa) is described. The surprising discovery of a Burnilia-species in Japan is the first record of a member of this subfamily outside the New World. As the generic assignment is beyond any doubts, this finding reveals a puzzling geographic distribution of this group. A natural – indigenous – occurrence of B. japonica in Japan versus a recent introduction e.g., by human traffic, is discussed. A phylogenetic study of the whole Plesiodelphacinae including the Japanese species is desired.

Introduction

The genus *Burnilia* Muir & Giffard, 1924, was established monotypically with the type species *Delphax pictifrons* Stål, 1864 described from Mexico (Stål 1864). Five more *Burnilia*-species have been described since: *B. belemensis* Muir, 1926 and *B. williamsi* Muir, 1926 from Brazil, *B. heliconiae* Muir, 1926, *B. longicaput* Muir, 1926 from French Guiana (see Muir 1926), and *B. spinifera* Fennah 1945 from French Guiana (Fennah 1945) with the subspecies *B. spinifera antillana* Fennah, 1959 from the Caribbean: St. Vincent Island (Fennah 1959). The genus *Burnilia* was hitherto considered as entirely

Neotropical. Due to the display of a cross-sectional circular post-tibial spur with well separated conical teeth Muir and Giffard (1924) placed *Burnilia* into the tribe Alohini Muir, 1915, still listed here in Metcalf (1943). Asche (1985a) described a second genus close to *Burnilia*, viz., *Plesiodelphax* with the type species *Plesiodelphax guayanus* Asche, 1985 from Brazil (type locality: Porto 14 de Mayo) and French Guiana. Moreover, Asche (1985a) removed *Burnilia* from the Alohini (the latter being integrated as junior synonym into the Delphacini: Asche 1985b), and established the subfamily Plesiodelphacinae for *Burnilia* and *Plesiodelphax*, based on characters regarded as autapomorphies (concerning hind wing vena-

tion, the special carination of the vertex, the arrangements of distal spine at the first post-metatarsus, and in the special configuration of the male genitalia, as described and discussed in Asche 1985b). The display of the post-tibial spur was rather regarded as "kelisioid" than as "alohinid" (Asche 1985a). In his phylogeny of Delphacidae, Asche (1985b), placed the Plesiodelphacinae above the level of Stenocraninae as the sistergroup of Delphacinae (see also Asche 1990). Mainly based on larval morphology, Emeljanov (1995) distinguished only three subfamilies of Delphacidae: Asiracinae, Ugyopinae and Delphacinae. The latter comprises seven tribes including Plesiodelphacini which were placed in his cladogram above the level of Stenocranini and considered as the sistergroup of a clade Tropidocephalini – Saccharosydnini plus Delphacini, - congruent with the hypothesis of Asche (1985b). However, Emeljanov's tribal classification is not fully adopted here, with consequence that plesiodelphacine taxa are still regarded as separate subfamily as suggested by Asche (1985b, 1990). The higher classification of Delphacidae has also been addressed by Hamilton (2006) who interpreted and supplemented mainly Emeljanov's data (Emeljanov 1995). Hamilton (2006) moved most subfamilies and tribes with the exception of Plesiodelphacinae to a single subfamily "Delphacinae". For Plesiodelphacinae he referred to Bartlett (2005) who reported about possible relationships of this group to Asiracinae. Urban et al. (2010) investigated the phylogeny of Delphacidae on the basis of molecular data and implications revealed from host plant associations, providing the first substantive molecular phylogeny of this family. According to their data, Plesiodelphacinae would possibly have derived from a level basally of Kelisiinae and Stenocraninae; however, as this hypothesis would have a substantial impact on the interpretation of morphological data as suggested earlier by Asche (1985b) and Emeljanov (1995), we here adopt the morphology-based phylogenetic hypothesis. A phylogenetic study for the whole group of Plesiodelphacinae is in preparation by the senior author.

Meanwhile several more plesiodelphacine species were discovered in the Neotropics, and are currently subject of a revision of the whole group (Asche, in preparation). The finding of persistent populations of a new *Burnilia* species in South Japan represents an enormous enlargement of the whole subfamily's range of distribution. Here we describ this new *Burnilia* species and provide information on its host plants and ecology.

Material and methods

The specimens were collected by sweeping or by visual search directly from the host plant, and preserved dry. Measurements and line drawings were made by using a Leitz stereomicroscope with camera lucida attachment. Genital structures were examined after the whole abdominal were macerated for 24 hours at room temperature in KOH, subsequently transferred to glycerine (for

drawings to glycerine jelly). Photographs were taken by the digital camera Canon50D with a MP-E 65mm Macro Photo Lens and by some compact digital cameras in the field, arranged by Paintshop Pro X4. The terminology used for bodily parts including male genitalia largely follows Asche (1985a, b; 1990), Holzinger et al. (2003), Hoch (2013), for female genitalia Bourgoin (1993), for wing venation Bourgoin et al. (2015).

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Taxonomy

Burnilia Muir & Giffard, 1924

Proterosydne: Crawford 1914: 570, nec Kirkaldy 1907: 130. Burnilia Muir & Giffard, 1924: 7. Type species: Delphax pictifrons Stål, 1864, [Mexico], by original designation.

Diagnosis (modified from Asche 1985a, b). As a plesiodelphacine genus, Burnilia is recognizable by the following combination of characters: head with vertex well projected in front of compound eyes, carination weakly developed or partly entirely missing; frons elongate and usually widest at frontoclypeal suture; antennal joints subcylindrical with elongate pedicel; head usually with boldly coloured contrasting blackish marks, either as transverse frontal stripe(s), or as longitudinal frontal stripe enclosing median carina; sides of head in front and/or above compound eyes partly with extended black patches; pronotum anterolaterally with a dark mark, in some species bearing waxy exudations; post-tibial spur "alohine", i.e., elliptical in cross-section bearing well separated cone-shaped teeth at the posterior margin; hind wings with anastomosis of M and Cu; drumming organ sexually dimorphic, males with elongate and erect apodemes of the second abdominal sternite and development of a "central plate" in the second abdominal tergite; diaphragm of male genital segment dorsally with conspicuous transverse spatula-shaped or subtriangular projections directed cephalad (probably as ventrocaudal support of the aedeagus); aedeagal complex devoid of a free suspensorium, dorsal base of phallotheca directly connected with ventral base of anal segment; aedeagus tubular, elongate, curved dorsally, central tube strongly sclerotized, phallotheca membranous, in most species subapically a single spinose or flag-like process; females ditrysic, i.e., full separation of copulation and oviposition duct; entry to prevaginal chamber mostly sclerotized, often forming a funnel-shaped guiding aid for the aedeagus.

Asche (1985a, b) considered the shape and carination of the vertex as well as the unique configuration of the male genitalia associated with the ditrysic female genitalia (diaphragm of the genital segment with a spatula-like

transverse plate directed interiorly, supposedly for guiding the aedeagus into the female copulatory duct) as autapomorphic for *Burnilia*. The newly discovered species from Japan displays these autapomorphies, and can therefore be regarded as a congener.

We refrain from the establishment of a separate subgenus for the Japanese species based on certain morphological differences from Neotropical *Burnilia* (see below) before a phylogenetic analysis of this taxon is available.

Distribution. Neotropical Region (6 species, one of which two subspecies), South East Palaearctic Region: Japan (one species described below, new record).

Burnilia japonica sp. n.

http://zoobank.org/23CFB02E-DB32-474A-8D89-4894670B3692 Colour plate 1, Figs 1–6

Description. Slender, medium-sized delphacid species of delicate appearance with strongly pale-dark contrasting colouration of the head.

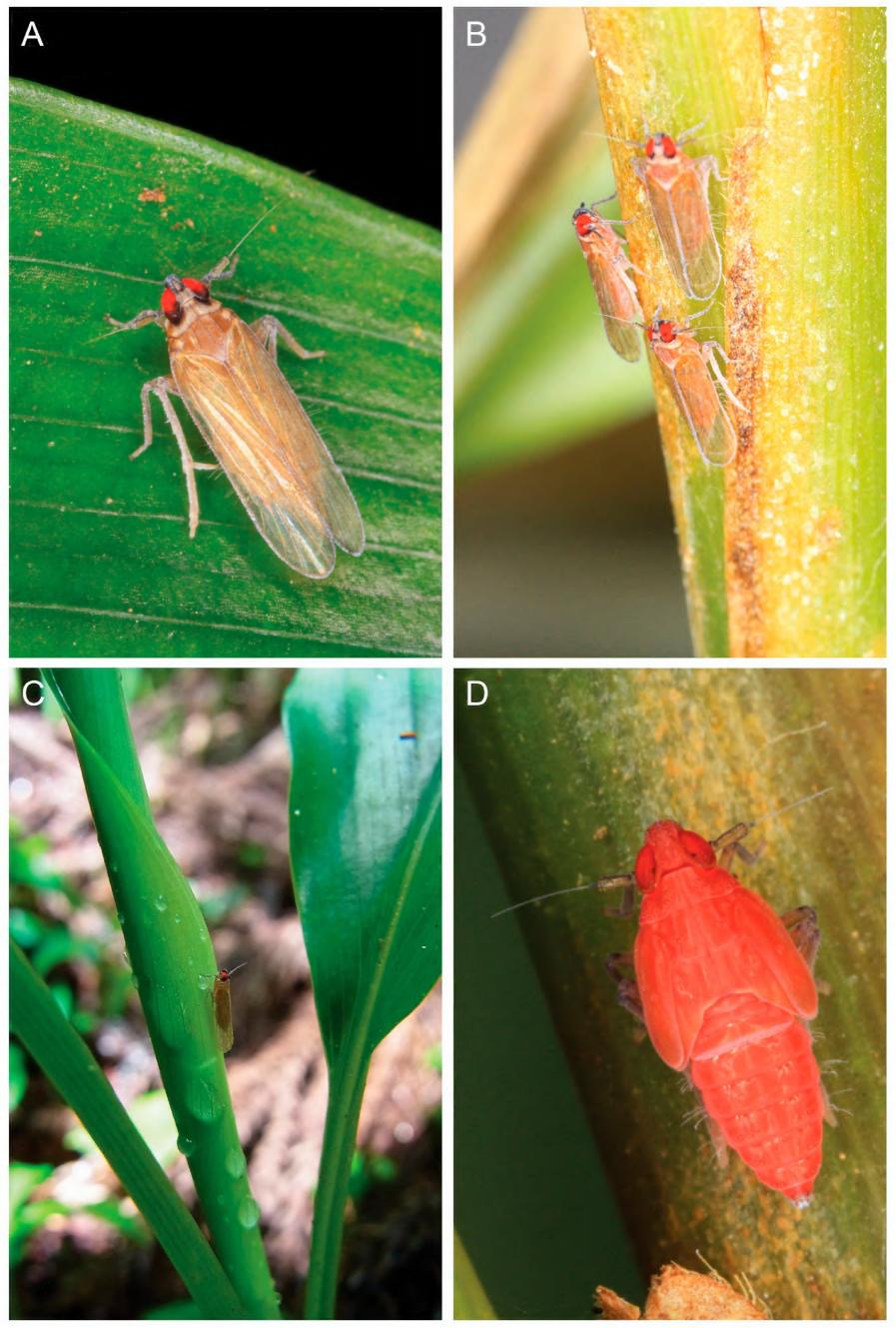
Length (from tip of head to apex of tegmina): Males (n=20): 4.0–4.4 mm (mean 4.2 mm); Females (n=20): 4.3–4.7 mm (mean 4.5 mm)

Colouration: Ground colour pale yellow to orange. Vertex pale yellow, with a narrow transverse dark brown to blackish stripe across the posterior margin of the anterior compartment; lateral margins, posterior corners and converging anterior carinae blackish brown; transition to frons as well as dorsal part of median frontal carina blackish. Frons pale yellow, lateral margins blackish, median carina centered in a narrow black-brown stripe. Post- and anteclypeus orange, median carina of postclypeus brownish. Rostrum orange with black tip. Antennae sordid orange-brown; scape distally fringed blackish-brown; pedicel anteriorly with a broad oblique brown stripe which is distally darker. Sides of head in front and dorsally of compound eyes broadly marked black, posterior corners above compound eyes blackish; compound eyes bright red; sides otherwise pale yellow to orange; ocelli centered in a brown spot; oblique genal carina anteriorly fringed brown; lower part of genae pale yellow; lamina mandibularis (lorae) orange. Pronotum sordid pale yellow, carinae of disk and posterior margin brownish, sides behind compound eyes anteriorly brown; laterodistal part of pronotum pale yellow, anteriorly with a blackish fringe. Mesonotum and tegulae sordid orange-brown. Tegmina translucent, smokey pale yellow or light sordid brown, veins light brown. Hind wings hyaline with brown veins. Legs orange to pale yellow, distal outer margin of tibiae brown. Abdominal tergites and sternites as well as male and female genitalia, mostly orange; ovipositor and posteromedian parts of tergite IX brown, anal style in males brownish, and females blackish.

Head and thorax: Head with large compound eyes, narrow vertex and frons; head including compound eyes about 3 times wider than vertex at base, about 0.8 times narrower than maximum width of pronotum. Vertex elon-

gate, narrow, medially about 1.87 times longer than wide at base, distinctly projected in front of compound eyes; lateral margins subparallel, slightly converging towards apex, apex in dorsal view truncate; compartments of vertex concave, limited by faint but well recognizable carinae; basal compartments elongate, anteriorly limited by anteriorly diverging carinae; anterior compartment rhomboid, lateral carinae converging towards apex and medially continuing as median frontal carina; transition of vertex to frons in lateral view in an almost right angle, apically slightly rounded. Frons elongate, apically rather narrow, continuously widening towards frontoclypeal suture, medially about 2.1 times longer than maximally wide, widest at frontoclypeal suture, basally about 3 times wider than apically, from medially about 1.3 times longer than postand anteclypeus together; lateral frontal carinae ridged, very slightly convex, in parts nearly straight, diverging from apex towards base; median frontal carina distinctly ridged, frontal surface in upper part shallowly concave, in lower part almost plain or slightly convex; frontoclypeal suture almost straight. Postclypeus vaulted, median carina ridged, lower part forming a nose-like projection (best seen in lateral view). Antennal joints subcylindrical, elongate, terete; pedicel about 2.8 times longer than scape, furnished with about 16 sensory plaques, arranged in 7 groups, partly in rows. Compound eyes large, in lateral view flat kidney-shaped, mediobasal incision above antennal base distinct, ocelli well developed; oblique genal carina sharply ridged. Pronotum about 3.6 times wider than medially long, carinae of disk sharply ridged, attaining posterior margin, lateral carinae slightly convex, diverging posteriorly; surface of disk shallowly concave. Mesonotum medially about 2.6 times longer than pronotum, carinae ridged, lateral carinae very slightly concave, diverging towards and attaining the posterior margin, median carina vanishing before reaching scutellum; surface of disk nearly plane. Tegulae well developed, in dorsal view about as long as wide. Tegmina elongate and narrow, about 4.5 times longer than maximally wide, widest shortly distad of nodal line, the latter in distal third; subapical cells small and narrow, inner cell (C5) slightly longer than outer one (C1), in membrane M branched into M1 and M2. Margin of hind wing with distinct notch at A1, M distally branched. Legs slender; hind leg with tibia about 1.25 times longer than tarsal joints together, laterally furnished with 2 spines, one close to base, the other shortly below midlength, distally with 5 spines: 2 rather small ones inside, 3 increasingly longer ones towards outside; post-basitarsus about twice as long as 2nd and 3rd post-tarsal joints together, distally with 5 spines: 4 in a row, one spine positioned anteriorly out of row; 2nd post-tarsal joint distally with 4 spines: the 3 inner ones forming an oblique row, the outer one distinctly longer.

Abdomen slightly depressed, hypopleurites subrectangular with straight outer margin. Male drumming organ with paired apodemes of the second abdominal sternite elongate, erect, slightly widening dorsally, nearly attaining tergites.



Colour plate 1. *Burnilia japonica* sp. n. **A.** Adult female (27. August 2013); **B.** Adults approaching each other (16. July 2014); **C.** Adult, on a rolled leaf of *Alpinia intermedia* (Yakushima; 20. August 2013); **D.** 5th instar nymph (body length ca. 2.7 mm) on potted host plant, *Alpinia intermedia* (13. July 2014).

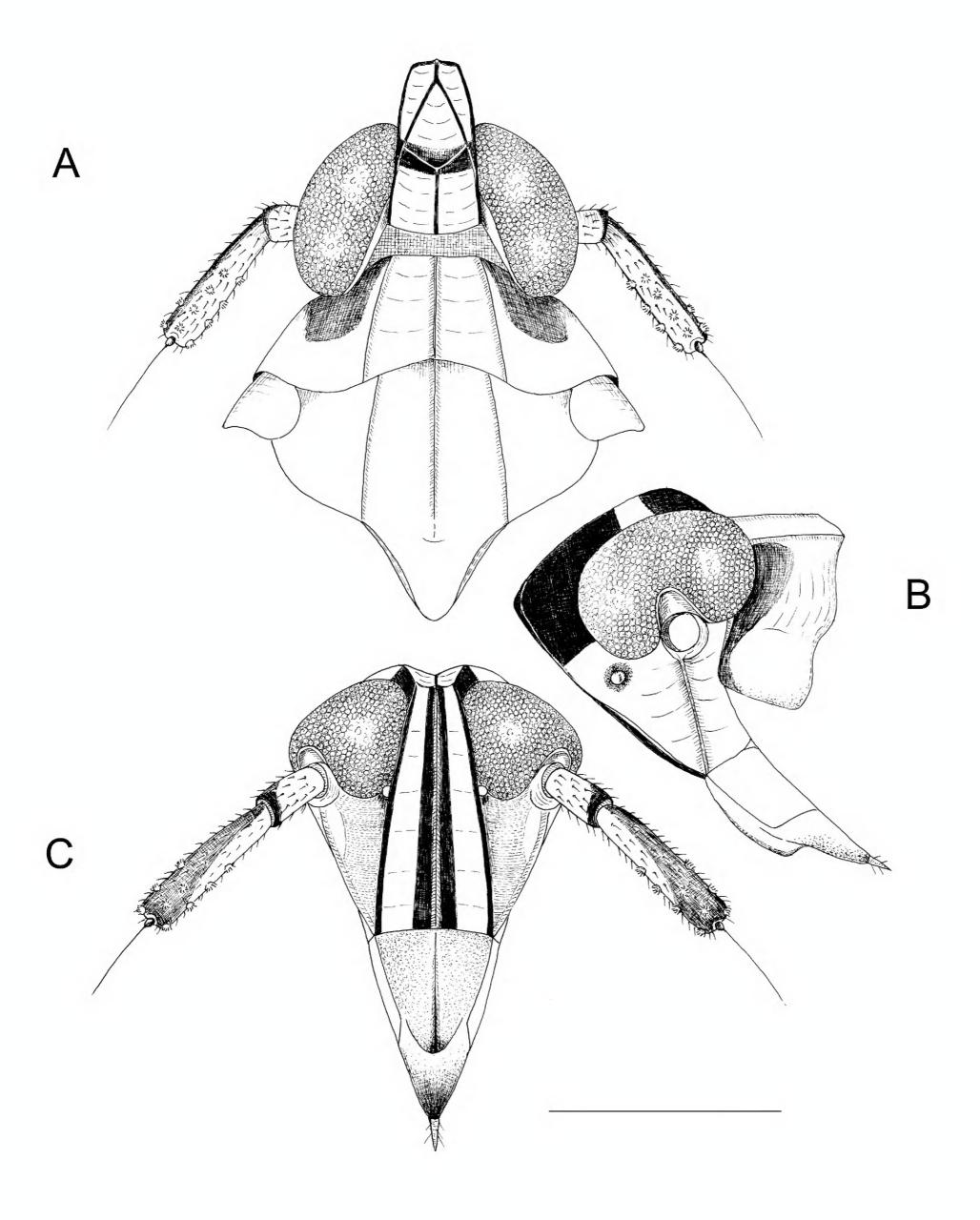


Figure 1. A. Head and thorax, dorsal view; B. Head, left lateral view; C. Head, frontal view; scale bar 0.5 mm.

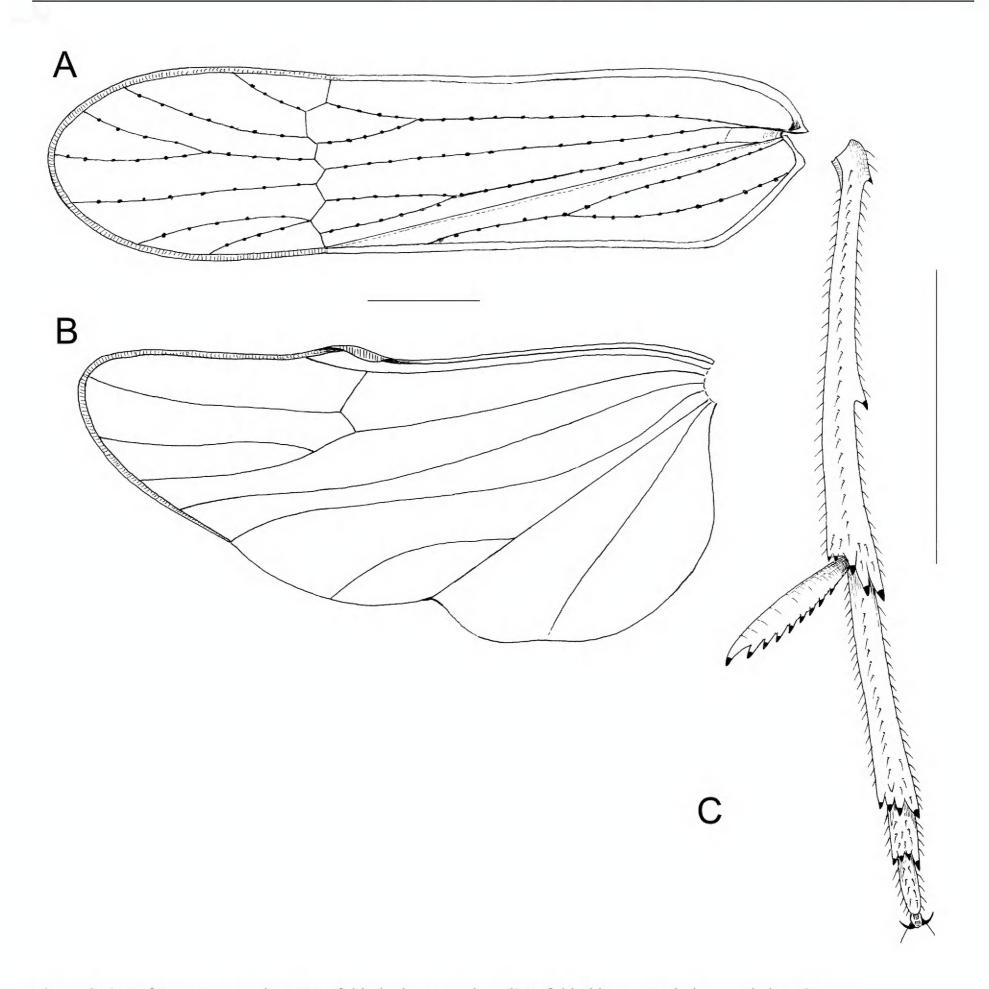


Figure 2. A. Left tegmen, venation; B. Left hind wing, venation; C. Left hind leg, ventral view; scale bars 0.5 mm.

Male genitalia: Genital segment in lateral view trapezoidal, ventrally about 1.3 times longer than dorsally, laterodorsal corners slightly produced, caudal margin nearly straight; in ventral view medially slightly longer than wide, mediocaudal margin straight with a small central knob; in caudal view ovoid, slightly higher than wide; diaphragm narrow, median sclerotized portions lobe-like with median membranous interruption. Aedeagus relatively short, when exposed hardly surpassing tip of anal segment, in lateral view curved dorsally; central sperm-conducting tube (sheath sensu Yang and Chang 2000) strongly sclerotized and ending in an apical phallotreme which is fringed by a crown of grooves and exposed to the left side; no free suspensorium: base of phallotheca connecting to anal segment strongly sclero-

tized forming phallobase sensu Yang and Chang (2000), otherwise phallotheca membranous, subapically on dorsal side slightly dilated and very finely serrate, on ventral side with a stronger sclerotized patch, in one of the examined individuals subapically on right dorsal side with a small sclerotized tooth directed dorsally; dorsally, immediately below the phallotreme on the left side, with a slender, apically pointed flag-like process which is almost semicircularly curved over the dorsal towards the right side, process subapically with small teeth. Anal segment, elongate, robust, shaft in ventral view about 1.7 times longer than maximally wide, widest caudally, ventrocaudal corners projected ventrally forming ear-like lobes, slightly asymmetrical; ventral surface membranous; anal style subconical, ventral side slightly concave,

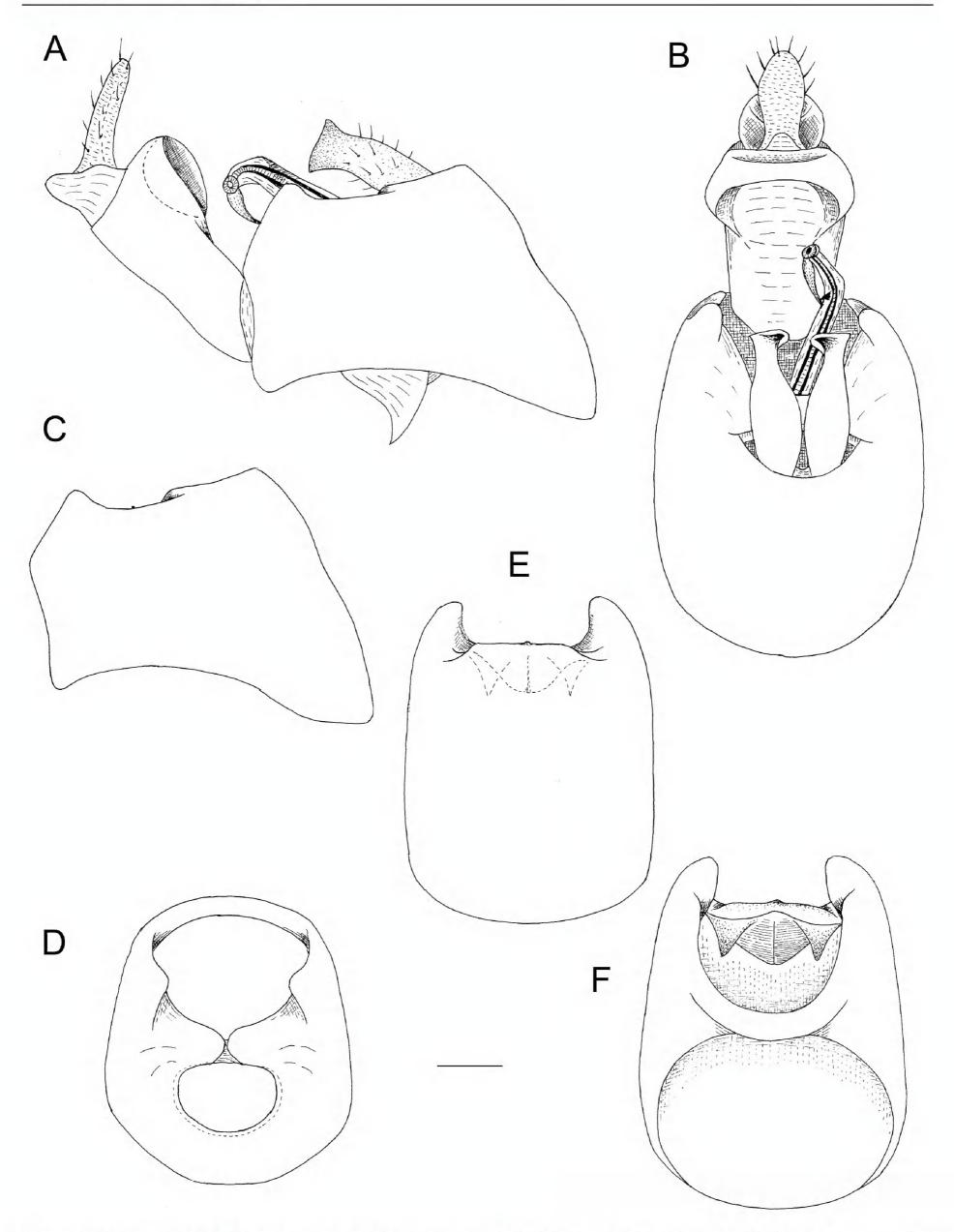


Figure 3. Male genitalia. **A.** Genital complex in left lateral view; **B.** Genital complex in ventral view; **C.** Genital segment in left lateral view; **D.** Genital segment in caudal view; **E.** Genital segment in ventral view; **F.** Genital segment in dorsal view; scale bar 0.1 mm.

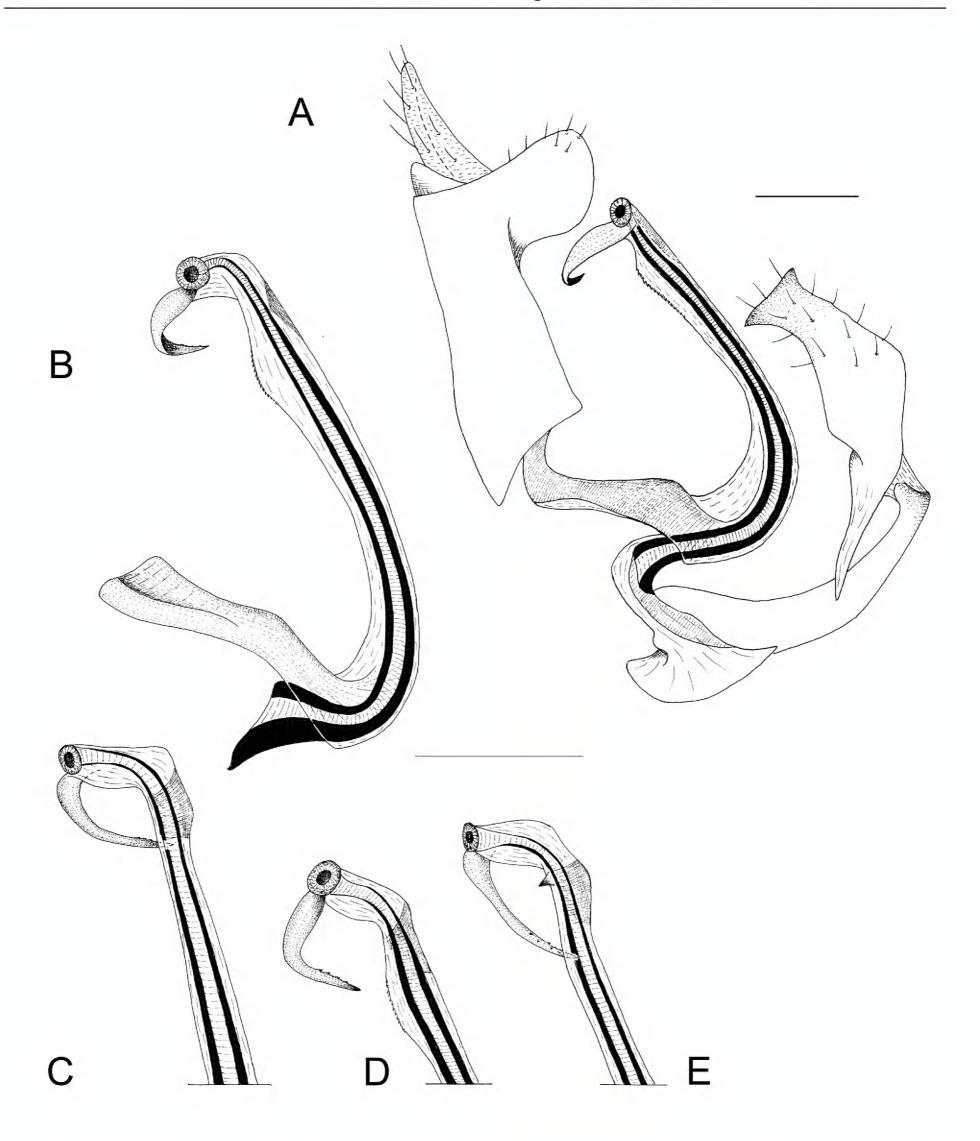


Figure 4. Male genitalia. **A.** Genital complex in left lateral view, genital segment removed; **B.** Aedeagus left lateral view; **C.** tip of aedeagus in ventral view; **D.** tip of aedeagus in ventral view, *versus* **C.** slightly twisted to left; **E.** tip of aedeagus in ventral view, another specimen, notice the short ridged spine; scale bars 0.1 mm.

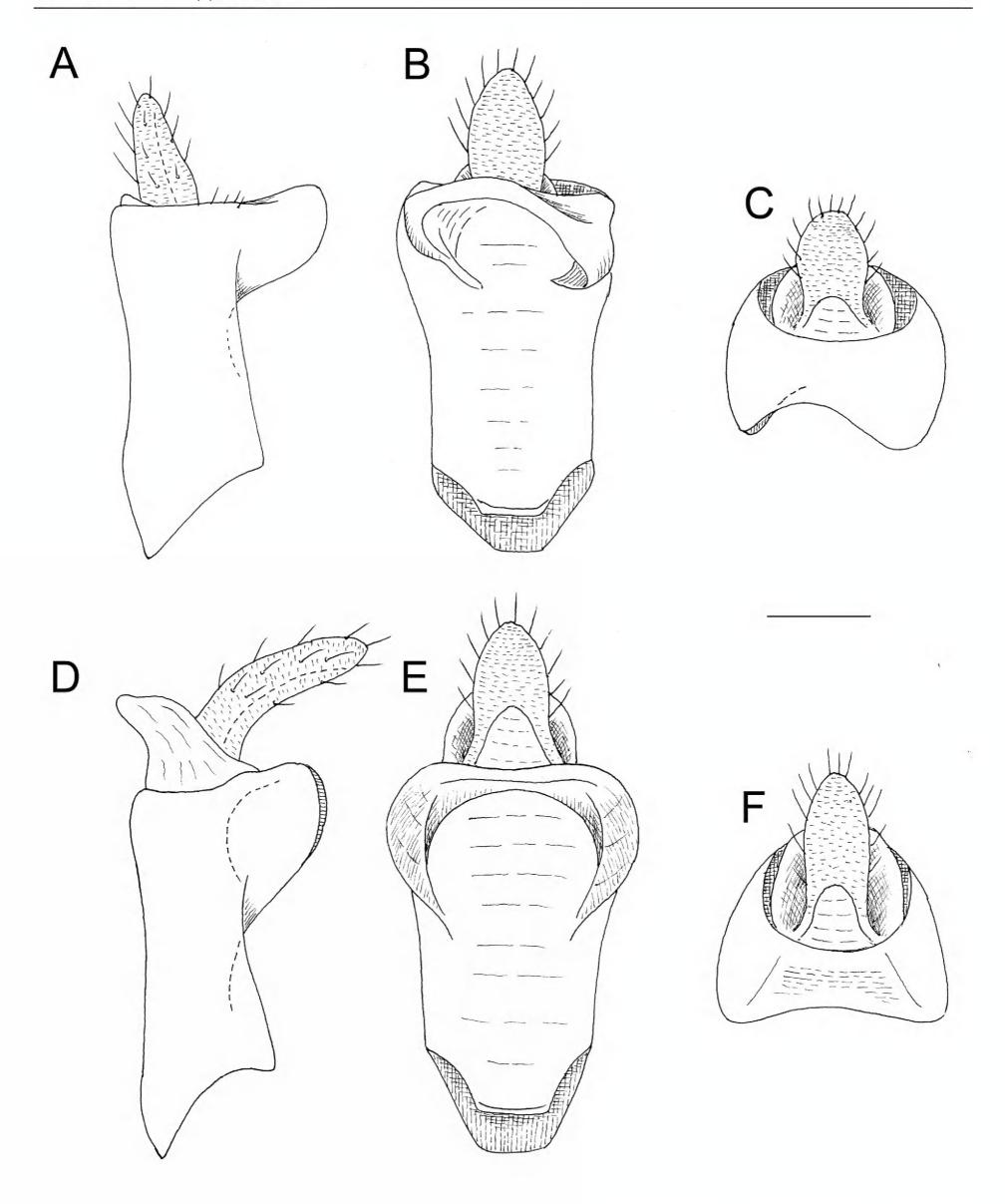


Figure 5. Male genitalia. **A–D**: ♂ 1, **D–F**: ♂ 2. **A, D.** Anal segment and anal style in left lateral view; **B, E.** Same in ventral view; **C, F**. Same in dorsal view; scale bar 0.1 mm.

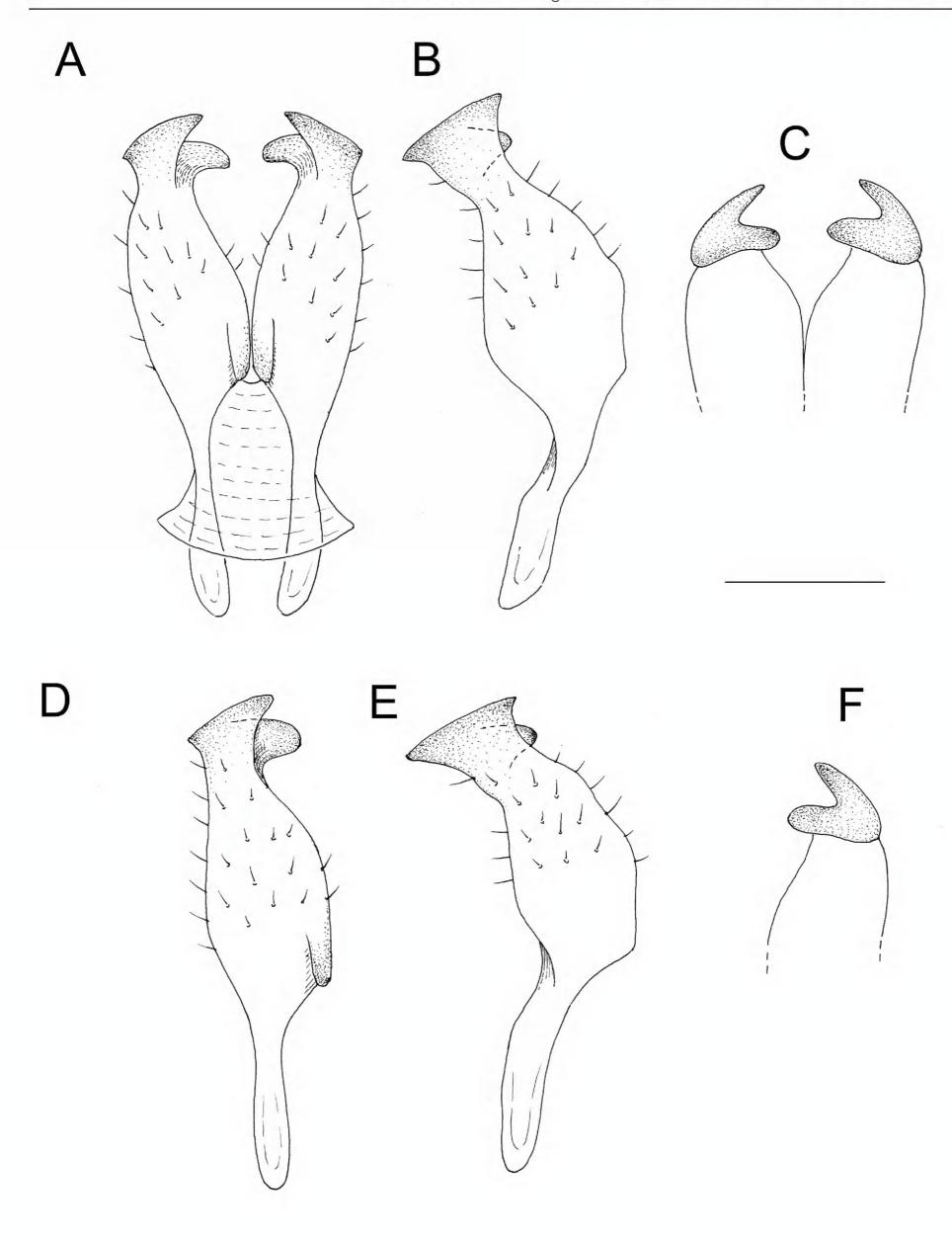


Figure 6. Male genitalia. **A–C:** ♂ 1, **D–F**: ♂ 2. **A, D.** Genital styles resp. left genital style in ventral lateral view; **B, E.** left genital style in left lateral view; **C, F.** left genital style, tip in caudal view; scale bar 0.1 mm.



Colour plate 2. Habitat of *Burnilia japonica* sp. n. **A.** Cedar forest floor, Yakushima Island, Japan; **B.** same locality, undergrowth of cedar forest, ferns interspersed with *Alpinia intermedia*.

about 4 times shorter than anal segment, mostly gently curved ventrally. Genital styles distinctly shorter than anal segment, in repose not attaining dorsolateral edges of genital segment, arising from a broad base and continuously narrowing towards apex, narrowest subapically, apically dilated into a bilobate tip; the inner apical lobe shorter than the outer one, apically rounded and pointing medially; the outer lobe ventrally and dorsally pointed, in lateral view forming a wide trapezoidal tip with nearly straight caudal margin.

Female genitalia: as in all Plesiodelphacinae ditrysic with clear separation of copulation and oviposition duct (Asche 1985a, b). Ovipositor slender, compressed, slightly curved dorsally, not surpassing the lateral edges of tergite IX; at base of ovipositor a sclerotized groove into the vagina guiding and supporting the aedeagus during copulation; gonoplacs large and relatively wide, fully enclosing gonapophyses VIII and IX, gonapophysis IX dorsally in distal third finely serrate; gonocoxae VIII elongate, slightly dilated and rounded at base; tergite IX laterocaudally slightly pointed; anal segment short and depressed, about as long as wide, anal style about as long as anal segment, ventrally concave and membranous.

Diagnosis. Burnilia japonica sp. n. can easily be distinguished from the New World species of the genus by the colouration of the frons: median carina broadly bordered by a blackish stripe versus from entirely devoid of colour patterns, or frons furnished by one or two transverse blackish stripes in Neotropical species. In B. japonica sp. n. the vertex displays a faint but distinct carination separating the two posterior from the anterior compartment; in the Neotropical species at least the median carina separating the basal compartments is strongly reduced or absent, in some species also the basal carinae limiting the anterior compartment are absent. B. japonica sp. n. is also unique by the possession of a relatively short and sturdy aedeagus (usually distinctly more slender and elongate in Neotropical species), by a flag-like semicircular subapical aedeagal process (forming a straight, slender spine in Neotropical species, if present), and by an anal segment with large ear-shaped lateroventral lobes (no such lobes are observed in the Neotropical species).

Distribution. Japan: Kyushu (south-westernmost area), Yakushima Island of the Osumi Isles and Okinawa Island (northern part) of the Ryukyus, endemic.

Hostplant, ecology, and biology (see Colour plate 2). In the extent of our field investigations on Yakushima Is. south of Kyushu, the host plant is restricted to a wild perennial zingiberaceous plant, *Alpinia intermedia* Gagnep. (Zingiberaceae: *gingers*) distributed in Japan and the East Orientalis growing on shady and wet forest floors of cedar afforestation or sometimes laurophyll forests. The occurrence of this *Burnilia*-species is usually strongly confined to narrow spots even in a same forest. Although two other species of Zingiberaceae, *A. formosana* K.Schum. and *A. zerumbet* (Pers.) (apparently introduced) are also found in same area, and are rather

dominant at sunny forest edges or at roadsides, *Burnilia japonica* has never been found on these plants, but exclusively on *A. intermedia*.

In the field, both nymphs and adults are found near the ground, on stems of the host plant below the level of fallen cedar leaves. Adults may appear from late July with a probable peak at mid- and late August on Yakushima Is.

Since late summer of 2013, M. Hayashi had been rearing several adults collected by Fujinuma, on potted ginger-lilies (*A. intermedia*) at his home near Tokyo. Adults were never observed to hibernate; thus it is assumed that overwintering occurs as eggs. Some nymphs were recognized in the following June, and a first adult appeared on July 5, 2014. The nymphs in every instar are wholly red, becoming vivid in last (5th) instar. On stems of the host plant, both adults and nymphs stand still with their heads directing upward and antennae fully stretching right laterally. Adults just after emerging are carmine red, gradually changing their colouration to yellowish with grey tinge. The compound eyes, however, remain brightly red with a black pseudopupil.

Etymology. The specific name refers to the geographical occurrence in Japan.

Material examined. Holotype & macropterous, Japan, Kagoshima Pref., Osumi Isles, Yakushima, Yudomari, 20.VIII.2013, S. Fujinuma (TUA). The holotype is deposited in the Laboratory of Entomology, Tokyo University of Agriculture, Japan.

Discussion

For the first time a representative of the plesiodelphacine Delphacidae, hitherto assumed to be confined to the New World, is recorded from the Old World, i.e., from warm-temperate and subtropical Japanese islands. The species is new to science, and beyond any doubt belongs to the genus *Burnilia* Muir & Giffard which is considered a monophyletic group. However, it appears to be unique in characters of the male genitalia displaying a relatively short aedeagal shaft with flag-like terminal process, an anal segment with large laterocaudal ear-shaped projections, and apically bifurcate genital styles. While in most New World *Burnilia*-species the carination of the vertex is strongly reduced or even absent, it is faintly present in the Japanese *Burnilia*, - possibly a plesiomorphic trait.

It is noticeable that the Japanese *Burnilia* species does not match the colouration patterns and the morphological display of any of the six described American *Burnilia*-species. Therefore it appears conceivable, even likely, that this species is in fact indigenous to the South Japanese Islands, and was just overlooked in previous surveys, although Japan including its southern islands must be regarded as comparatively well studied concerning its fauna, including planthoppers.

The extension of the range of occurrence of *Burnilia*-species to the Old World is remarkable, and represents a prime example of trans-Pacific disjunction. The question arises whether this zoogeographic pattern is due to dispersal or vicariance events.

Examples of recent New World introductions to Europe across the Atlantic are known, e.g., the (presumed invasive) American delphacine *Prokelisia marginata* (Osborn) feeding on the Poaceae-species *Spartina mari*tima (Curtis) Fernald into coastal saltmarshes of Portugal and Slovenia (Curtis) (Seljak 2004). Viceversa the European delphacine Conomelus anceps (Germar) feeding on Juncaceae recently appeared in North America (Wheeler and Hoebeke 2008). For more examples of transatlantic migration see Bartlett et al. (2014). Natural long distance trans-Pacific dispersal of small arthropods by e.g., wind, rafting, has been documented by Gressitt 1961). In planthoppers, natural trans-Pacific dispersal with successful colonizations is assumed for the ancestors of the – now – endemic faunas of Pacific island groups such as Hawai'i (Asche 1997). In Hawai'i, however, also recent immigrant planthopper species from Oriental-Australian sources towards the East, and *viceversa* from the New World towards the West have been recorded (e.g., Asche 2000). We, however, are not aware of any Oriental or New World delphacid species that successfully crossed (by whatever means) the entire Pacific in either direction and established viable populations.

Although we cannot fully exclude the possibility of a recent introduction of a Burnilia species into Japan from a Neotropical source, and although a species-level phylogeny of the Plesiodelphacinae is still missing, we lean towards vicariance as the underlying mechanism of the currently observed distribution pattern in Burnilia. This hypothesis is also supported by the fact that Burnilia japonica feeds only upon a wild zingiberacous plant, Alpinia intermedia Gagnep., distributed from southwestern Japan to Taiwan, China and the Philippines. This host plant is most likely native in Japan; it probably has never been introduced, and also not been cultivated as ornamental or decorative plants. The localization and endemism of this Burnilia-species very likely reflects a natural distribution. Neotropical *Burnilia*-species (as far information is available) feed on, *Heliconia* spp.. (Heliconiaceae, - in older literature listed in Musaceae). In the Neotropics Burnilia-species have been collected "within new, curled leaves (like those seen in figure 8c) before the leaves have uncurled' (Ch.Bartlett, personal communication). For the second plesiodelphacine genus *Plesiodel*- *phax* and its type-species *P. guayanus* Asche a host plant is unknown.

A rather similar distribution pattern is observed in another group of Delphacidae, namely taxa of the tribe Saccharosydnini, with 3 entirely Neotropical genera, and one more genus, *Saccharosydne* Kirkaldy, 1907, with type-species *S. saccharivora* (Westwood, 1833) described from the West Indies which contains some more species from the New World, but also a single species from the Old World, namely *S. procerus* Matsumura, 1931, described from Japan and reported from China, S. Russia, Taiwan, Korea, and probably Vietnam (Ch. Bartlett, personal communication).

Similar biogeographic patterns have also been reported from other groups of organisms, (e.g., Diptera, Keroplatidae: Matile 1990; plants: Heads 1999). An interesting hypothesis to explain trans-Pacific, trans-tropical disjunct distributions has been suggested by McCarthy (2003), assuming a "closed Pacific in the Upper Triassic-Lower Jurassic" some 200 Million years ago. The opening and expansion of the Pacific may be the vicariant event which eventually led to the split between the Japanese and Neotropical Burnilia lineages; however, this assumption appears rather speculative due to the high geological age concerned.

Although a far more recent distributional pathway across the Beringian bridge in Cenozoic times is theoretically conceivable (V.M. Gnezdilov, personal communication), there is no evidence for a historic occurrence of this group in the Holoarctic Region.

Fossil records for Delphacidae in general are sparse, and mainly concern geologically younger periods like the Eocene (e.g., Szwedo et. al. 2004). For Plesiodelphacinae fossils are unknown.

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